

Seasonal abundance of the Monte Albo cave salamander *Speleomantes flavus* in Italy

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Abstract

The Monte Albo cave salamander, *Speleomantes flavus*, is the species endemic to the namesake massif located in the northeastern part of Sardegna, Italy. *Speleomantes* are the only plethodontid species in Europe, a genus composed of eight troglophilic species living in epigean and subterranean environments. Most ecological studies on these species deal with species occupancy (i.e., presence/absence), while studies aiming to identify drivers for their abundance are lacking. Here, we present the first study aiming to determine which ecological factors influence the abundance of *S. flavus*. We identified three main hypotheses: (1) salamanders are more abundant where microclimatic conditions are the most suitable for their physiological requirements; (2) *Speleomantes* are more abundant where prey richness is the highest; and (3) salamanders tend to avoid potential predators. Our results suggested that cave air temperature, humidity, and illuminance are strongly affected by season, and individuals of *S. flavus* tended to aggregate in relatively cold and humid areas not far from the cave entrance. For most *Speleomantes*, there was a significant correlation between their abundance and the presence of the considered invertebrate species. This study produced the first information on which ecological features affect the abundance of *S. flavus* individuals. Additional studies extending to further *Speleomantes* populations and species may support our hypotheses, including factors not considered here.

Keywords

Abundance, *Hydromantes*, microhabitat, Plethodontidae, predator, prey, subterranean

Introduction

European cave salamanders (genus *Speleomantes*) are the only representative of the family Plethodontidae in Europe, of which the large majority is distributed throughout North America (Wake 2013). *Speleomantes* are a group of eight species endemic (or sub-endemic) to Italy: seven species (*S. ambrosii*, *S. italicus*, *S. flavus*, *S. supramontis*, *S. imperialis*, *S. sarrabusensis*, and *S. genei*) are distributed on mainland Italy and Sardinia, while *S. strinati* occurs in Italy and a small portion of the French Provence (Lanza et al. 2006). *Speleomantes* are fully terrestrial amphibians with direct development and are characterized by the absence of lungs (Lanza et al. 2006). These specific features make *Speleomantes* very selective in terms of microclimatic conditions, as they require relatively low temperature and high moisture to guarantee the proper development of their eggs and to efficiently respire and osmoregulate through their skin (Spotila 1972; Lunghi et al. 2015b; Ficetola et al. 2018). These microclimatic conditions can be found in surface environments only during limited periods (mainly in spring and autumn), while they occur in deeper areas of many typologies of subterranean environments all year round (Culver and Pipan 2019). This circumstance was probably one of the leading causes that promoted the colonization of subterranean environments by *Speleomantes*, making them one of the most common troglophile vertebrate species in Europe and likely one of the main drivers of allochthonous organic matter that contributes to sustaining the local subterranean community (Lavoie et al. 2007; Barzaghi et al. 2017).

The colonization of subterranean environments by *Speleomantes* may have provided individuals with both advantages and disadvantages. Besides the pursuit of prolonged and constant suitable microclimatic conditions (Culver and Pipan 2019), *Speleomantes* may have the benefit of switching their trophic position at the top of the local trophic web (Manenti et al. 2020), strongly reducing the probability of being predated by most of their natural predators (Lunghi et al. 2018e; Di Nicola et al. 2024). On the other hand, individuals from subterranean environments found themselves the top predators in an oligotrophic ecosystem (Culver and Pipan 2019), being forced to move towards surface environments to increase the chance of finding potential prey (Manenti et al. 2015; Lunghi et al. 2018d), although being subjected to higher predatory risk (Manenti et al. 2016; Lunghi et al. 2018c; Lunghi and Corti 2021).

We present the first ecological study on multiple populations of The Monte Albo cave salamander *S. flavus* (Fig. 1A). In this study, we want to assess which are the main ecological factors affecting the abundance of salamanders over an entire calendar year. Specifically, we want to test the following hypotheses. The microclimatic selection hypothesis (MSH) predicts that *Speleomantes* tend to occupy cave sectors showing the best environmental conditions to maintain higher efficiency for their cutaneous respiration (Spotila 1972), so we expect a higher abundance where the most suitable conditions are realized (Ficetola et al. 2018). The best foraging hypothesis (BFH) predicts that *Speleomantes* tend to aggregate in areas characterized by the highest availability of food resources to increase the ecological opportunity and to minimize the effort to

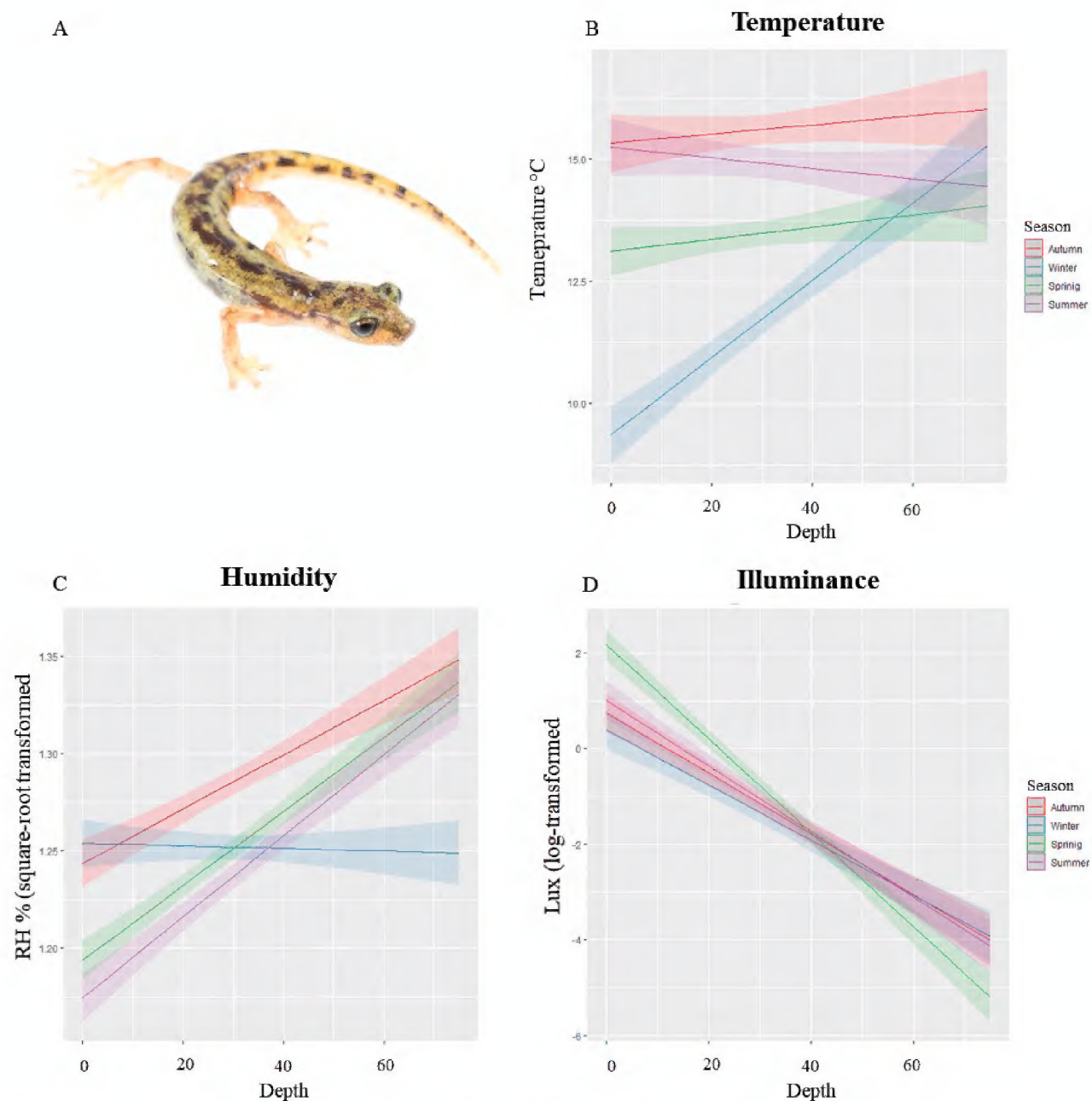


Figure 1. **A** an adult *Speleomantes flavus*. Photo credits: Simone Giachello **B–D** plot showing results of GLMM analyses performed on cave microclimatic conditions. Results show the seasonal trends for **B** air temperature (°C) **C** air humidity (%; square-root transformed) and **D** illuminance (lux; log-transformed). Shaded areas indicate 95% CI.

catch prey (Lunghi et al. 2018d; Lunghi et al. 2020c; Cianferoni and Lunghi 2023). The predation risk hypothesis (PRH) predicts that *Speleomantes* reduce their abundance in the presence of potential predators, and therefore, low individual abundance is expected when predators' diversity is higher.

Methods

Dataset and survey methods

We analyzed the data published by Lunghi et al. (2020a). This dataset contains information on the cave microclimate and on individuals of *Speleomantes flavus* (Fig. 1A) collected within seven natural caves located in the Monte Albo massif (Sardinia, Italy).

A total of 77 surveys (at least two per season) were conducted throughout the year, starting from October 2015 (autumn) to June 2016 (summer). A single researcher surveyed the inner cave environment, collecting data every three linear meters, starting from the entrance until the cave's end or the point in which the survey became too hard (e.g., too tight passages, employment of speleological equipment). Every cave section of 3 linear meters (hereafter, sector) was surveyed with a constant effort of 7.5 minutes per sector to standardize data on *Speleomantes* abundance (Banks-Leite et al. 2014). During sector surveys, the presence/absence of potential prey and predators was also recorded (see below). At the end of each sector (i.e., at its maximum distance from the cave entrance), three microclimatic variables were measured. Air temperature (°C) and relative humidity (%) were measured at the ground and 2.5 m of height using a TDP92 thermo-hygrometer (accuracy: 0.1 °C and 0.1%); this allowed us to take into account potential variation due to stratification of the microclimate (de Freitas 1982; Badino 2010). Maximum and minimum illuminance (lux) were measured in the most illuminated and the darkest points using a DVM1300 light meter (minimum recordable light: 0.1 lx). During sector surveys, we counted all salamanders observed; when possible, individuals were captured to determine the sex and to collect data on body size (snout-vent length; mm). Adult males were recognized by the presence of the mental gland, their characteristic secondary sexual trait (Lanza et al. 2006). No apparent external morphological character can easily distinguish between adult females and juveniles; their discrimination is only possible based on size (Lanza et al. 2006). Salamanders with snout-vent length (SVL) ≥ 55 mm were considered adult females, while those < 55 mm SVL were considered juveniles (Lunghi et al. 2018b). Some individuals ($N = 110$) were marked using a visual implant alpha tag (Lunghi and Veith 2017), and just 10 individuals were captured twice over a year (Lunghi et al. 2020a). Considering this low recapture rate, we assume that the dataset is not affected by the repeated preferences recorded for the recaptured individuals, and it genuinely provides an overview of the preferences of the studied populations. Within each sector, the presence of four cave invertebrates was also recorded. We considered the crane flies and the snail *Oxychilus oppressus* potential prey (Lunghi et al. 2018a; Lunghi et al. 2020b; Cianferoni and Lunghi 2023). The spiders *Meta bourneti* and *Tegenaria* sp. were considered potential predators, as some reports documented the predation on juvenile individuals of *Speleomantes* (Manenti et al. 2016; Lunghi and Corti 2021).

Analyses of cave microclimate

We first assessed the occurrence of specific microclimatic gradients during each season using Generalized Linear Mixed Models (GLMM) with R Studio (Douglas et al. 2015; Lunghi et al. 2015a; Team 2020). For each microclimatic variable (temperature, humidity, and illuminance), we averaged the two measures performed at the end of each cave sector. Before their use, the humidity was square-root transformed, and illuminance was logarithmically transformed to better fit a normal distribution, allowing their use in models with Gaussian distribution. In the first GLMM, we used

the average temperature as the dependent variable, while the sector depth (i.e., its maximum distance from the cave entrance), the season, and the interaction between them were independent variables. Due to multiple visits, cave and sector identity were included as random variables. Two additional GLMMs were performed, replacing the dependent variable once with mean humidity and once with mean illuminance; the other variables remained the same. Likelihood ratio tests were used to test the significance of model variables (Kuznetsova et al. 2016).

Analyses of *Speleomantes flavus* abundance

We used GLMM with negative binomial distribution to assess whether abiotic and biotic factors affect the abundance of *S. flavus* (Brooks et al. 2017). This type of model better fits zero-inflated count data that do not follow a normal distribution (Saphiro-Wilk test always $P > 0.05$). The count data on *S. flavus* abundance was used as the dependent variable, while season and its interaction with sector depth were independent factors. The season is considered a proxy for the variability of the cave microclimatic conditions as it strongly affects the inner cave environment, especially in its first parts (Lunghi et al. 2015a). Instead of adding each microclimatic variable as a further independent variable (making models more complex), we here used the “season” to represent specific microclimatic conditions (see Results, but also Lunghi et al. 2015a). The presence of potential prey and predators were added to the model, as they may have opposing effects on the salamanders’ abundance. Cave and sector identity were used as random factors. We used the Likelihood ratio test to assess the significance of the model variables. We then built a second model without including the non-significant variables; we chose the best one based on AIC criterion and the Likelihood ratio test. When the two models did not significantly diverge, we chose the most parsimonious (i.e., the less complex one). This analysis was repeated to assess the effect of those variables on each salamander group separately (adult males, adult females, and juveniles); to perform these GLMMs, unsexed adult individuals were discarded to avoid bias.

Results

Cave microclimate

The average mean sector temperature was significantly affected by the season ($F_{3,11.71} = 45.53$, $P < 0.001$), sector depth ($F_{1,192.61} = 8.78$, $P = 0.003$), and by the interaction between season and sector depth ($F_{3,1531.56} = 215.59$, $P < 0.001$). The mean sector temperature was significantly lower in winter ($\beta = -5.93$, SE = 0.14, $P < 0.001$) and spring ($\beta = -2.13$, SE = 0.13, $P < 0.001$). No difference was observed for summer ($P = 0.694$). The mean sector temperature was significantly higher near the cave entrance in summer ($\beta = -0.02$, SE < 0.01, $P < 0.001$), and in deeper sectors in winter ($\beta = 0.07$, SE 0.01, $P < 0.001$). No significant interaction was observed for spring ($P = 0.659$) (Fig. 1B).

The average mean sector humidity was significantly affected by the season ($F_{3,1544.64} = 66.34, P < 0.001$), sector depth ($F_{1,82.13} = 113.76, P < 0.001$), and by the interaction between season and sector depth ($F_{3,1544.62} = 48.17, P < 0.001$). The mean sector humidity was significantly lower in spring ($\beta = -0.06, SE = 0.01, P < 0.001$) and summer ($\beta = -0.07, SE = 0.01, P < 0.001$). No difference was observed for winter ($P = 0.198$). The mean humidity was slightly lower in cave deeper sectors during winter ($\beta < -0.01, SE < 0.01, P < 0.001$), while in spring and summer it was slightly higher in deeper sectors ($\beta < 0.01, SE < 0.01, P = 0.003$ and $\beta < 0.01, SE < 0.01, P < 0.001$, respectively) (Fig. 1C).

The average mean sector illuminance was significantly affected by the season ($F_{3,1540.22} = 22.5, P < 0.001$), sector depth ($F_{1,281.84} = 74.82, P < 0.001$), and by the interaction between season and sector depth ($F_{3,1540.18} = 14.10, P < 0.001$). The mean sector illuminance was significantly higher in spring ($\beta = 1.04, SE = 0.18, P < 0.001$), while no difference was observed during other seasons ($P > 0.05$). The mean sector illuminance was generally higher near the cave entrance ($\beta = -0.04, SE < 0.01, P < 0.001$), especially in spring ($\beta = -0.03, SE < 0.01, P < 0.001$). No significant interaction was observed with other seasons ($P > 0.25$) (Fig. 1D) (see Table 1).

Table 1. Estimated regression parameters, standard errors, *t*-values, and *P*-values for the GLMM analysis on the cave microclimatic conditions.

Dependent variable	Predictors	Estimate	Standard error	<i>t</i> -value	<i>P</i> -value
Temperature	Intercept (Autumn)	16.380	1.050	15.591	<0.001
	Winter	-5.932	0.141	-41.966	<0.001
	Spring	-2.127	0.132	-16.097	<0.001
	Summer	-0.056	0.141	-0.393	0.694
	Depth	-0.002	0.004	-0.500	0.618
	Winter*Depth	0.069	0.004	17.171	<0.001
	Spring*Depth	0.003	0.004	0.659	0.510
	Summer*Depth	-0.021	0.004	-5.246	<0.001
Humidity	Intercept (Autumn)	1.237	0.014	87.403	<0.001
	Winter	0.009	0.007	1.289	0.198
	Spring	-0.058	0.007	-8.722	<0.001
	Summer	-0.070	0.007	-9.810	<0.001
	Depth	0.002	<0.001	8.223	<0.001
	Winter*Depth	-0.001	<0.001	-7.072	<0.001
	Spring*Depth	0.001	<0.001	2.928	0.003
	Summer*Depth	0.001	<0.001	3.565	<0.001
Illuminance	Intercept (Autumn)	0.080	0.606	0.133	0.897
	Winter	-0.380	0.195	-1.950	0.051
	Spring	1.040	0.182	5.707	<0.001
	Summer	0.241	0.195	1.234	0.217
	Depth	-0.041	0.006	-6.352	<0.001
	Winter*Depth	0.006	0.006	1.146	0.252
	Spring*Depth	-0.025	0.005	-4.828	<0.001
	Summer*Depth	-0.005	0.006	-0.850	0.395

Speleomantes flavus abundance

We observed 831 individuals of *Speleomantes flavus*, of which 589 (94 adult males, 138 adult females, and 357 juveniles) were captured (Table 2). The best model did not include variables related to the two spider species and the *Oxychilus oppressus* (Table 3). The abundance of *Speleomantes flavus* was significantly lower in summer ($\beta = -1.51$, SE = 0.39, $P < 0.001$) and winter ($\beta = -1.23$, SE = 0.49, $P = 0.006$), while no difference was observed for spring ($P = 0.394$). *S. flavus* was more abundant towards the cave entrance ($\beta = -0.05$, SE = 0.02, $P = 0.006$) and in sectors in which crane flies were present ($\beta = 0.72$, SE = 0.21, $P < 0.001$). A tendency to increase its abundance in deeper sectors was observed in summer ($\beta = 0.04$, SE = 0.02, $P = 0.02$), while no effect was observed during the other seasons ($P > 0.569$) (Fig. 2A).

The best model for adult males did not include the variables related to the two prey species (*O. oppressus* and crane flies) and the interaction between sectors and seasons (Table 3). The abundance of adult males was significantly lower in winter ($\beta = -2.39$, SE = 0.79, $P = 0.002$), while no difference was observed during the other seasons ($P > 0.436$). Males were slightly less abundant near the cave entrance ($\beta = -0.04$, SE = 0.01, $P = 0.012$), while they were more abundant in sectors where *M. bourneti* ($\beta = 1.55$, SE = 0.56, $P = 0.006$) and *Tegenaria* sp. were present ($\beta = 1.24$, SE = 0.47, $P = 0.009$) (Fig. 2B).

The best model for adult females only included the variable related to the season (Table 3). The abundance of adult females was significantly lower in winter ($\beta = -1.55$, SE = 0.53, $P = 0.004$), while no difference was observed in other seasons ($P > 0.124$) (Fig. 2C).

The best model for juveniles did not include the variables related to crane flies and the spider *Tegenaria* sp. (Table 3). The abundance of juveniles was significantly lower in summer ($\beta = -0.99$, SE = 0.49, $P = 0.04$), while no difference was observed in other seasons ($P > 0.135$). Juveniles were more abundant in sectors where *M. bourneti* ($\beta = 0.82$, SE = 0.41, $P = 0.048$) and *O. oppressus* ($\beta = 0.93$, SE = 0.23, $P < 0.001$) were present. No apparent difference was observed for juvenile seasonal distribution ($P > 0.05$), but they showed a tendency to increase their abundance near the cave entrance in summer ($\beta = 0.04$, SE = 0.02, $P = 0.052$) (Fig. 2D).

Discussion

We demonstrated that the abundance and the distribution of the Monte Albo cave salamanders within caves mainly depend on microclimatic features (Lunghi et al. 2014; Ficetola et al. 2018), which are strongly affected by climate seasonality. The considered microclimatic variables (air temperature, humidity, and illuminance) vary along the transect from the entrance to the deep cave zone (i.e., with increasing cave depth; Fig. 1) and are strongly dependent on climatic conditions occurring in adjacent surface environments (Culver and Pipan 2019). The microclimatic conditions characterizing the area nearest the entrance mostly resemble those occurring in surface

Table 2. Captured individuals of *Speleomantes flavus*. For each season, we indicate the number of adult males, adult females, juveniles, unsexed adults, and the total of observed individuals.

Season	Adult males	Adult females	Juveniles	Unsexed adults	Total individuals
Autumn	20	26	61	30	137
Winter	2	6	29	23	60
Spring	57	90	229	148	524
Summer	15	16	38	41	110

Table 3. Parameters related to model selection for *Speleomantes* abundances. We here compare the full model with a reduced model that does not include nonsignificant predictors assessed with a Likelihood Ratio Test.

Group	Model	Df	AIC	BIC	Log-Likelihood	Deviance	Chi-Square	ΔDf	P-value
<i>Speleomantes</i> total	Reduced	12	2008.10	2075.10	-992.06	1984.10			
	Full	15	2007.40	2091.10	-988.68	1977.40	6.76	3	0.08
<i>Speleomantes</i> males	Reduced	10	594.24	650.03	-287.12	574.24			
	Full	15	599.66	683.35	-284.83	569.66	4.58	5	0.47
<i>Speleomantes</i> females	Reduced	7	703.84	742.90	-344.92	689.84			
	Full	15	705.04	788.74	-337.52	675.04	14.80	8	0.06
<i>Speleomantes</i> juveniles	Reduced	13	1199.70	1272.20	-586.84	1173.70			
	Full	15	1200.10	1283.80	-585.07	1170.10	3.54	2	0.17

habitats in both magnitude of fluctuation and intensity. At the same time, external influences decrease, and the microclimate becomes stable with increased cave depth (Lunghi et al. 2015a). This was particularly true for air temperature, which showed an annual fluctuation of about 5 °C in the most profound areas (60–75 m). In contrast, within the first 15 m from the cave entrance, there was an annual variation of almost 20 °C (Lunghi et al. 2020a). The cave air temperature showed a marked and opposite trend towards the deep cave areas during summer (negative) and winter (positive), while in spring and autumn the temperatures slightly increased with depth from the cave entrance (Fig. 1B). Concerning the other microclimatic variables, we detected a constantly increasing trend for humidity, and a constantly decreasing trend for illuminance (Fig. 1C, D). The only exception for humidity occurred in winter, as seasonal precipitation reduced the gap between the conditions occurring at the two extremities of the cave environment (Fig. 1C).

Our analyses supported the predictions of the microclimate selection hypothesis (MSH). The abundance of *Speleomantes flavus* was strongly affected by seasonality (Fig. 2), one of the main factors responsible for microclimatic fluctuation within the first meters of caves (Lunghi et al. 2015a). Such influence remained evident even if individuals were analysed separately (Fig. 2). During summer, the season with the harsher environmental conditions for *Speleomantes* (Ficetola et al. 2018), individuals were generally less abundant and tended to concentrate in the most profound cave areas, where favourable microclimatic conditions occur year-round (Fig. 1). During

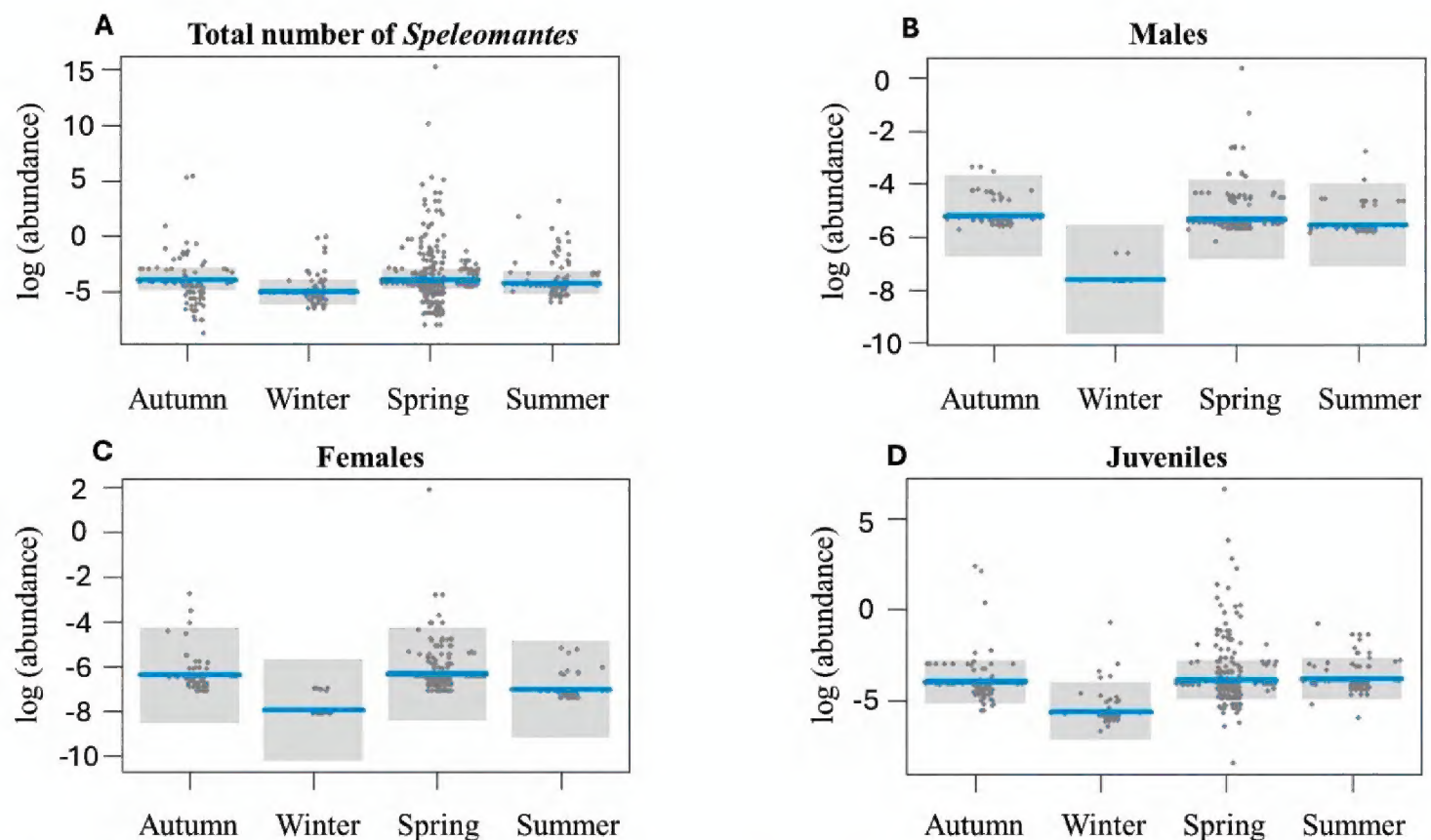


Figure 2. Plot showing results of *S. flavus* abundance during seasons **A** total number of *Speleomantes* **B** adult males **C** adult females; and **D** juveniles. Y axes show the log transformed abundances. Blue horizontal line represents mean values, while shaded areas indicate 95% CI.

winter, invertebrate abundance significantly decreases in surface environments (Driesen et al. 2013), and adults probably have no reason to leave the highly suitable deep cave areas to reach sub-optimal conditions if prey availability is scarce.

Our second hypothesis, the best foraging hypothesis (BFH), was partially supported, as only adults did not show a significant correlation with the presence of prey. Considering that most of the caves in the Palearctic region are oligotrophic (Culver and Pipan 2019), *Speleomantes* tend to concentrate in the cave areas that support the highest prey abundance, namely those nearest the entrance (Lunghi et al. 2017; Lunghi et al. 2020b). This is particularly true for young individuals, who prefer to occupy these sub-optimal microclimatic conditions to find higher prey availability (Salvidio and Pastorino 2002; Ficetola et al. 2013). We currently lack data to adequately explain the observed non-significant correlation between prey species and adult abundance, but we have a hypothesis that deserves to be tested. In our study, we only used the presence of two potential prey, the crane flies and the snail *Oxychilus oppressus*. Since *Speleomantes* exhibits an opportunistic and generalist foraging behavior (Cianferoni and Lunghi 2023), individuals may be more attracted by the quantity rather than the simple presence of potential prey species (Manenti et al. 2015). Future studies considering this feature may support our BFH hypothesis.

Our third and final hypothesis, the predation risk hypothesis (PRH), was not supported, as no *Speleomantes* group (males, females, juveniles, and overall) reduced its abundance in the presence of predators. *Speleomantes* are epigean mesopredators that have switched their trophic position to the top of the trophic pyramid in colonized

subterranean environments (Manenti et al. 2020). Contrary to our expectation, the abundance of adult males and juveniles was positively related to the presence of these predator spiders. One of these potential predators is the orb-web cave spider *Meta bourneti*, a widespread species on Monte Albo (Lunghi 2018). *Meta* spiders are considered a good proxy for prey availability in subterranean environments (Manenti et al. 2015), and their positive correlation with some groups of *Speleomantes* can be an artifact due to the indirect correlation with prey abundance. Particularly, we expected to observe a negative relationship between juveniles and cave spiders due to the documented predation events (Manenti et al. 2016; Lunghi and Corti 2021). The predation risk for juvenile *Speleomantes* is probably lower than expected. Indeed, the only observed cases of predation of *Speleomantes* by cave spiders report salamanders that were likely to fall into the spider web, which gives a consistent advantage to the spider. Some other epigean predators can use the first meters of the cave as a foraging area (Lunghi et al. 2018e; Di Nicola et al. 2024), but this is not an everyday event, and thus, it was not considered in our analysis. Additional studies are required to test whether predators' abundance can better predict *Speleomantes* abundance.

We conducted the first study that provided information on the ecological factors that influence the abundance of *Speleomantes flavus* in caves. Our results identified microclimatic suitability as the main driver, followed by the presence of specific invertebrate species. The highest activity of *S. flavus* occurs during the seasons in which the climatic conditions are the most suitable for the species (i.e., spring and autumn), and within the subterranean environments, individuals tend to be more abundant near the cave entrance, where prey availability is the highest. We did not observe a negative effect due to the presence of potential predators, supporting the hypothesis for the apical position of *Speleomantes* within the cave trophic pyramid. Our preliminary results should represent the starting point for future studies that consider additional ecological factors (e.g., prey/predator abundance) and test these same hypotheses in other *Speleomantes* species.

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